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STUDIES UPON THE BIOLOGICAL SIGNIFICANCE OF ANIMAL COLORATION

II. A REVISED WORKING HYPOTHESIS OF MIMICRY

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ALTHOUGH zoologists know that detailed resemblance in outward appearance may occur between different species of insects which are not closely related, they do not agree in their interpretation of the facts they observe. Present knowledge, indeed, justifies nothing more than tentative explanations of mimicry; but, in this matter, observations recently reported[1] limit one's freedom of choice, since they appear to bear directly upon the validity of current hypotheses reviewed in the following pages.

The first attempt to interpret mimetic resemblance as a result of natural selection was made by H. W. Bates,[2] who writes:

> What advantage the Heliconidæ possess to make them so flourishing a group, and consequently the objects of so much mimetic resemblance, it is not easy to discover. . . . It is probable that they are unpalatable to insect enemies. . . . They have all a peculiar smell. I never saw flocks of the slow flying Heliconidæ in the woods persecuted by birds or dragon flies, to which they would have been an easy prey;

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[1] Longley, "The Colors and Color Changes of West Indian Reef-fishes," *Jour. Exp. Zool.*, 1917. It happens that the present paper will appear slightly before that cited.

[2] *Trans. Linn. Soc. Lond.*, Vol. 23, p. 510.

> nor, when at rest on leaves, did they appear to be molested by lizards or the predaceous flies of the family Asilidæ, which were very often seen pouncing on butterflies of other families. If they owe their flourishing existence to this cause, it would be intelligible why the Leptalidæ, whose scanty number of individuals reveals a less protected condition, should be disguised in their dress, and thus share their immunity.

Bates himself points out the fact that "some of the mutual resemblances of the Heliconidæ seem not to be due to the adaptation of the one to the other, but rather, as they have a real affinity, . . . to the similar adaptation of all to the same local, probably inorganic conditions." Thus the application of his hypothesis was limited from the beginning.

Fritz Müller[3] showed how those instances of resemblance which his predecessor ascribed to the influence of Lamarckian factors might be aligned with the Darwinian hypothesis. In Meldola's[4] translation of his original paper his idea is expressed as follows:

> What benefit can one species derive from resembling another, if each is protected by distastefulness? Obviously none at all, if insectivorous birds, lizards, etc., have acquired by inheritance a knowledge of the species which are tasteful or distasteful to them—if an unconscious intelligence tells them what they can safely devour and what they must avoid. But if each single bird has to learn this distinction by experience, a certain number of distasteful butterflies must also fall victims to the inexperience of the young enemies. Now if two distasteful species are sufficiently alike to be mistaken for one another, the experience acquired at the expense of one will likewise benefit the other; both species together will only have to contribute the same number of victims which each of them would have to furnish if they were different.

Recent years have been marked by a tendency upon the part of some observers[5] to extend the bounds of the Müllerian associations, until in a given fauna a large proportion of the insects which show the same color combination are included in one bionomic group. Scores of species have, indeed, been assigned to some, and it has been alleged that very many types from the same region show the influence of one or another of the dominant Müllerian aggregations. Müller's hypothesis, however, has not attained preeminence solely by extension to newly discovered cases of resemblance, but has prospered in many instances at the direct expense of the Batesian conception. Its changed fortune depends largely upon Dixey's[6] discovery of mimetic attraction, or reciprocal mimicry.

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[3] *Kosmos*, May, 1879, p. 100.

[4] *Proc. Ent. Soc. Lond.*, 1879, p. xxvii.

[5] Marshall and Poulton, "The Bionomics of South African Insects," *Trans. Ent. Soc. Lond.*, Vol. 41, pp. 287–584.

This relation, which it is held exists between many insects previously considered typical Batesian couples, suggests that the observed resemblance involves mutual adjustment. But the idea that each species introduces into its own pattern elements characterizing that of the other, and thus contributes actively to the development of a common type of coloration, is intelligible in terms of the mimicry hypotheses, only if the superficial resemblance so attained is mutually advantageous. Whatever justifies change in the interpretation of fact lies here; for, if it be assumed in the beginning that the likeness noted must have arisen either through the action of Batesian or Müllerian factors, it must be admitted that the notion of mutual advantage seems more fitly associated with the latter: two species, each of which enjoys marked immunity, seem better able to force reciprocal concessions in their achievement of resemblance, than they should, if there were great disparity in their means of defence.

Perhaps the most obvious suggestion from Dixey's research is not, after all, that a closer approximation to truth may possibly be attained through reclassification of mimetic resemblances, but that an intergrading series of alleged Batesian and Müllerian mimics is perfectly conceivable, in which no known test could possibly determine the occurrence of a natural break. Hence there would seem to be only historical reasons for maintaining the two categories.

It is noteworthy that neither hypothesis to which reference has been made was in its original form an attempt to explain the existence of conspicuous creatures. The sole concern of each was the interpretation of resemblances, which were later commonly considered mere incidents in the attainment and use of warning colors. This shifting of emphasis from "likeness which is perfectly staggering"[7] to conspicuousness, which failed to elicit a single outspoken comment in the original papers of Bates and Müller, is distinctly chargeable to Wallace,[8] who extended his hypothesis of the functional conspicuousness of bright colors, until it included the facts of mimicry.

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[6] *Trans. Ent. Soc. Lond.*, 1894, pp. 249–334.

Abbott H. Thayer[9] has proposed an explanation of the resemblance between unrelated species of butterflies, which is consistent with his thesis that the foremost function of animal coloration is concealment. This hypothesis is Darwinian in principle, but in practise is directly opposed to current selectionist opinion. It is purely speculative, and is stated as follows:

> It is surely conceivable that in a certain region, one particular form of flower-scenery representation may furnish such advantage to butterflies as to cause many widely separated species to become modified till they wear a common aspect, and it is conceivable also that there would be one common form of wing that would best lend itself to this scheme.

More recently Thayer[10] adds that in the paper from which the excerpt above is taken he ascribed more importance to butterflies' resemblance to flowers, as compared to their rendering of scenery, than he should at the later date; but this necessitates no modification of his idea that mimicry is mere incidental resemblance between species, which, through selection based upon the obliterative effect of their coloration, conform ever more closely to one ideal representation of their common background.

If the Darwinian ranks are divided upon the question of the prevalence of conspicuous types of coloration, similar though less open dissension appears among their opponents. To Piepers,[11] for example, specific coloration is in large part a visible token of internal organization determined from time immemorial, a result of orthogenetic evolution capable, however, of being accelerated or retarded by external conditions. To Packard[12] it represented a racial response of organism to environment, and mimicry seemed an effect of exposure to conditions of the same kind. But if evolutionary processes be largely beyond the control of external agents, and species spring from species through internal reorganization, as one configuration follows another in the kaleidoscope, one should anticipate that many color combinations of exaggerated conspicuousness might result. If, upon the other hand, the development of color and pattern be determined by animals' environment, their coloration may well repeat dominant notes from their surroundings. Hence it is not surprising to find that Packard expresses hearty appreciation of Thayer's discoveries, and Piepers, despite his anti-Darwinian attitude, might have much in common with Wallace and Poulton. Thus the full series of contradictions is rounded out, and the unsettled state of opinion concerning mimicry, or indeed the whole matter of animal coloration, is apparent, for the two qualities, utility and conspicuousness, openly or tacitly affirmed or denied, may be ascribed in every possible combination to the color and pattern of a single organism.

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[7] Bates, *l. c.*, p. 507.

[8] Darwinism, p. 239. Macmillan and Co., 1891.

[9] *Trans. Ent. Soc. Lond.*, Vol. 42, p. 557.

[10] See Thayer, Gerald H., "Concealing Coloration in the Animal Kingdom," Appendix *B*, p. 251. Macmillan and Co., 1909.

It may apparently be stated safely without qualification that the bright colors of tropical fishes as a class are correlated with the animals' habits, and, in the case of all but red, distinctly repeat tones characterizing their normal environment. But, other things being equal, no one will maintain that any system of external pigmentation could be less conspicuous than one conforming to this principle. Therefore, among these creatures at least, the occurrence of bright colors in contrastive patterns is not inconsistent with the idea that the forms that display them are as inconspicuous as may be under the conditions in which they live. It is this fact that necessitates a review of hypotheses of animal coloration that postulate conspicuousness; for one cannot safely disregard the suggestion that principles applicable to one group of animals may be valid also in the case of others.

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[11] "Mimikry, Selektion und Darwinismus." Leiden, 1903.

[12] *Proc. Amer. Philos. Soc.*, Vol. 43, p. 421.

It is of interest to note that Chapman[13] studied the birds of Trinidad under favorable conditions and observed that distinct types of coloration marked those of different habits. The most brilliant species occupy the most exposed positions in the treetops. More sedentary forms inhabiting the body of the trees are largely green, and brown predominates in the coloring of those that climb upon the tree-trunks, frequent the undergrowth near the forest border, or live upon the forest bottom.

These ecological records are a mere incident, a by-product of their author's activity. Through lack of detail they possess no great intrinsic value, but are highly significant in their present setting. Mention should also be made of Potts'[14] observation that shrimps living symbiotically with crinoids upon the Australian reefs repeat the colors of the forms with which they are associated. That comparable facts regarding other groups of animals are not available is immaterial. If the bright colors of tropical birds, fishes and some crustacea repeat those of the animals' respective environments and minister to the inconspicuousness of their possessors, it is of interest to inquire what data and reasoning support the contention that in insects similar combinations bear a different relation to the colors about them and discharge another function.

It appears first, from the statements of a number of their more prominent advocates, that there are fundamental theoretical objections to the hypotheses of warning coloration and mimicry.

Poulton[15] remarks that the acquisition of an unpleasant taste or smell, together with a conspicuous appearance, is so simple a form of protection, and yet *ex hypothesi* so absolutely complete, that it seems remarkable that more species have not availed themselves of this mode of defence. He argues that if once their potential vertebrate enemies were driven to eat any such insects in spite of their unpleasant taste, they would almost certainly soon acquire a relish for what was previously disagreeable, and the insects would be in great danger of extermination, having in the meantime become conspicuous by gaining warning colors. He concludes that if this reasoning is correct, it is clear that this mode of defence is not necessarily perfect, and that it depends for its apparently complete success upon the existence of relatively abundant palatable forms: in other words, its employment must be strictly limited.

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[13] *Bull. Amer. Mus. Nat. Hist.*, Vol. 6, pp. 19–20.

[14] Carn. Inst. Wash., *Papers Dept. Mar. Biol.*, Vol. 9, pp. 71–96.

[15] *Proc. Zool. Soc. Lond.*, 1887, p. 192.

Dixey[16] encounters the same difficulty in his consideration of Batesian mimicry. He observes that in this relation the advantage is all on the side of the edible mimicking species, whose existence is, indeed, a source of danger to the form mimicked, inasmuch as any experience gained by tasting the former would be used to the detriment of the latter. From these considerations he believes that such an association can exist only when the numbers of the one species are insignificant in comparison with those of the other. Upon this point he is in essential agreement with Wallace,[17] who states that mimicry has been shown to be useful only to those species and groups that are rare and probably dying out, and would cease to have any effect should the proportionate abundance of mimic and model be reversed.

Here, then, are two hypothetical types of association whose persistence admittedly depends upon the maintenance of definite though undetermined ratios between their components. Hence it devolves upon those who hold that the assumed relations are real, to outline some system by which the due proportion of protected and unprotected forms might be maintained through the interaction of natural factors.

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[16] *Trans. Ent. Soc. Lond.*, 1897, pp. 317–332.

[17] *Westminster Review*, Vol. 32, N. S., p. 35.

In an attempt to avoid this preliminary difficulty Poulton declares that it has always been recognized that an insect may be distasteful to one vertebrate enemy, but palatable to another. He suggests a different counterbalancing limit, which he admits would certainly in time become identical with the other. He argues that a vertebrate enemy may be forced by stress of hunger to eat an unpalatable insect, by implication asserts that this adaptability of potential enemies of forms tending to assume warning colors would limit the number of species developing them, and considers the truth of his suggestion confirmed by experimental tests.

It seems, however, that as long as warning coloration confers any advantage, other species should move in the same direction, for the same reasons that those did in which it first appeared. The number of warningly colored species should therefore increase until the situation conceived by Poulton materialized. But in that event the experimental proof that hungry animals are not so fastidious as those that are well fed is insufficient to meet the exigencies of the situation; for one has no reason to believe that animals which might become adjusted to the new condition would confine themselves to a diet of insects whose warning coloration was recently acquired, and would leave intact the vested interests of those that first attained it. Indeed, if one is permitted to speculate, it seems not wholly unreasonable to anticipate a swing of the pendulum in the other direction, so that conspicuous forms might face the possibility of almost complete extinction. This is suggested by the well-known fact that interspecific adjustments are not rigid, and that a state of approximate equilibrium is frequently modified by climatic or other factors, and restored only after a series of more or less definite oscillations. Examples in point are furnished by Howard's[18] observations upon ichneumon flies and their primary and secondary parasites, and more particularly by those of Forbes[19] and Bryant[20] upon the feeding habits of birds.

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[18] "New Nature Library," Vol. 7, Pt. 1 (The Insect Book), p. 68. New York, Doubleday, Page and Co.

In his paper, which has been cited above, Dixey was not discussing the validity of the mimicry hypotheses and has not attempted to explain what limits the numbers of a mimic in proportion to those of its model. Wallace also failed to elucidate the mystery, leaving his readers to find the way out of their difficulty as they might best be able. Search elsewhere for helpful suggestion in the matter yields little of value. Poulton[21] holds that ichneumon flies are particular enemies of the larvæ of "protected" Lepidoptera, but this idea need not be taken very seriously at present, for it is apparently based upon the observation of a high proportion of parasitized individuals among such forms rather than upon comparative statistics covering "unprotected" species as well. Even if it were true, while it would bolster the warning color hypothesis, it would aggravate the situation regarding Batesian mimicry. Therefore only one conclusion is possible: The theoretical objections they themselves have raised are not adequately met by spokesmen for the two hypotheses.

What observed facts support the contention that many animals are made conspicuous and profit by the striking combinations of color they display, should next be determined.

In 1867 Wallace[22] suggested before the Entomological Society of London that, as a rule, brilliantly colored larvæ are distasteful to birds, expressed his desire for information and his gratification, if any who kept birds, particularly indigenous species, would make experiments with different larvæ to ascertain which were eaten and which rejected. Members of the society and others have repeatedly acted upon his suggestion and commonly agree that the results of the experiments support his hypothesis, whose application has meanwhile been greatly extended. But the spirit in which the observed facts are interpreted precludes all possibility of the main inference drawn from them being seriously considered by any unprejudiced critic who examines the argument.

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[19] "The Regulative Action of Birds upon Insect Oscillation," *Ill. State Lab. Nat. Hist.*, Bull. No. 6.

[20] "The Condor," Vol. 13, 1911, pp. 195–208.

[21] "The Colors of Animals," p. 182. New York, D. Appleton and Co., 1892. For additional data, see *Trans. Ent. Soc. Lond.*, Vol. 41, p. 337.

[22] *Proc. Ent. Soc. Lond.*, 1867, pp. lxxx–lxxxi.

If a dull-colored insect be eaten, this is held by implication to lend strong support to the hypothesis of warning coloration; for palatable insects must be inconspicuous or be destroyed. If, upon the contrary, such an insect be rejected, its distastefulness may be a useless character, an accident of metabolism, or vestigial, or may be related to functional distastefulness in preceding stages of the life history; in any case "it must be remembered that an unpleasant attribute must always appear in advance of the warning coloring,"[23] so the result is not inconsistent with Wallace's suggestion. Again, if a bright-colored insect be rejected, this accords with his contention; and finally, if such a one be accepted, experimenters are prone to agree with J. Jenner Weir[24] who writes:

> But I am by no means inclined to attach undue importance to this fact, because the birds, being in a state of confinement, might readily be expected to eat insects, which in a state of nature, with a less limited choice, they would reject.

It is unnecessary to review these experiments in detail and to attempt to evaluate them, for this has already been done thoroughly by McAtee,[25] who shows their utter futility by comparing typical observations upon caged birds with the facts revealed by analysis of the stomach contents of wild specimens of the species experimented upon. Regarding information from such sources as that last-mentioned he writes:

> Since this evidence is sufficient in itself and since experimental data must be supported by it, why perform the experiments? The same time spent in collecting trustworthy data regarding the natural food

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[23] Poulton, "The Colors of Animals," p. 176.

[24] *Trans. Ent. Soc. Lond.*, Vol. 7, Ser. 3, p. 22.

[25] *Proc. Acad. Nat. Sci. Phila.*, 1912, pp. 281–364.

habits of animals would bring much greater returns, and the result would be truth, not imaginative inferences from abnormal behavior.

Before concluding the discussion of this matter it should be stated that even if it were proved that bright-colored insects are distasteful, it might not be inferred fairly that they are conspicuous, or that their coloration has a specific warning (aposematic) function. Feeding experiments under ideal conditions might determine the presence or absence of distastefulness, and show to what extent it is correlated with the display of color combinations of a particular sort. But even a high degree of correlation between unpalatability and gaudy coloration proves that the latter is conspicuous, no more than the demonstration that an unknown substance has the approximate *hardness* of gold proves that it has the same *specific gravity;* for brightness, or vividness of coloration, and conspicuousness are incommensurable.

Except in Thayer's contributions, confusion upon this point has prevailed from the beginning, when Wallace used interchangeably the expressions, "brilliantly colored larvæ" and "caterpillars conspicuous by their lively coloration." But the assumption that some animals are conspicuous, or, in other words, that while their habits remain the same their average visibility might be greatly diminished by another system of coloration than that they possess, can neither be adequately defended nor refuted, until the results of such exhaustive studies of animals' habits as have rarely been attempted are available. The distribution of animals must be studied intensively, for the division of the world into provinces and the subdivision of these into their major components by gross dissection is not a technique of sufficient refinement to discover the essential relations between organism and environment.

Passing to another phase of the matter, the value of recorded observations upon the conspicuousness of insects may be shown very clearly.

Bates saw no Heliconidæ attacked by dragonflies or other predaceous insects which often pounced upon butterflies of other families. But Poulton[26] finds, to state it mildly, that "there is good reason for believing that such attacks are not rarely made, and that predaceous insects are important enemies of aposematic butterflies." He also writes[27] of the Batesian hypothesis:

> This was not, as has been generally supposed, originated by Bates during his years of observation in the Valley of the Amazon. It arose in his mind after his return home, when he came to examine his collection and to reflect upon his experiences.

Under these circumstances the uncorroborated testimony of this witness concerning matters which are not known to have been carefully investigated in the Brazilian wilderness and are not determinable from the study of preserved material is of little immediate consequence. Among subjects regarding which his opinion can at present be held only in slight esteem, and concerning which he expressed himself in other communications than his original paper upon mimicry, the inherent conspicuousness of bright colors may be justly included.

The positive assertions in the following quotation describing conditions observed by an entomologist in British Guiana are also instructive; the same is true of their author's naïve conclusion.

W. J. Kaye[28] writes:

> The forest is dark and gloomy, and throughout the greater part of the year excessively damp owing to a superabundant rainfall. The character of the vegetation is always the same, as even in the dry season the trees are never otherwise than a fresh green. It is not surprising, therefore, that practically the whole of the Lepidoptera, excepting, of course, the several species of *Morpho,* present a very uniform, somber tone of coloration. Even the very fine and brightly colored *Heliconius catharinæ, H. astydamia* and *H. egeria* do not strike one in their surroundings as being particularly gaudy, and one is bound largely to admit the assertion of Abbott H. Thayer that many species we call conspicuous are not really so in their natural surroundings. It must, however, have been quite impossible for nature to have evolved such

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[26] *Trans. Ent. Soc. Lond.,* Vol. 41, p. 328. See also Vol. 44, pp. 323–409.

[27] "Essays on Evolution," p. 211. Oxford, Clarendon press, 1908.

[28] *Trans. Ent. Soc. Lond.,* Vol. 44, p. 412.

minutely close resemblance in unrelated groups without the aid of Müllerian mimicry.

It remains to state that among Lepidoptera different species have their characteristic attitudes of rest, frequent different places, fly at different levels, and are active at different times in the day. Even the two sexes of some species, and these are commonly dimorphic forms, do not haunt the same stations. It is certainly a pregnant fact, which we may accept since Wallace[29] gives independent testimony to the same effect, that Bates[30] observed many, apparently scores, of species, in which, as he says, the sun-loving males flaunted their gaudy hues in open places, while their respective females, soberly clad, frequented the forest shades.

These facts and others that might be cited are indications of diversity of habit among insects comparable with that which among fishes is correlated with the display of different types of inconspicuous coloration. They suggest that in this group as well, external pigments are distributed among species according to an intelligible system other than that whose existence is commonly inferred. But if this should eventually prove to be true, we must have an explanation of mimicry without appeal to the concept of warning colors.

Such a hypothesis has in fact been formulated by Punnett,[31] for in spite of his apparent belief in the conspicuousness of many species of butterflies it happens that he lays no stress upon it in his consideration of the origin of mimetic resemblance. His hypothesis, as he fully recognizes, is at present little more than naked suggestion. It is ingenious, is stated attractively in the current idiom of genetics, and is effectively displayed against a background of destructive criticism of its predecessors, from which it differs in minimizing the influence of nat-

[29] *Trans. Ent. Soc. Lond.*, Vol. 2, Ser. 2, pp. 253–264.

[30] "The Naturalist on the River Amazon," p. 291. Reprinted, New York, D. Appleton and Co., 1892.

[31] "Mimicry in Butterflies." Cambridge, University Press, 1915.

ural selection. It proposes an entirely new explanation of mimicry in the following terms:

> If we assume that sudden and readily appreciable variations of the nature of "sports" turn up from time to time, and if these variations happen to resemble a form protected by distastefulness so closely that the two can be confused by an enemy which has learned to avoid the latter, then there would appear to be good grounds for the mimicking sport becoming established as the type form of the species. . . . On this view natural selection in the form of the discriminating enemy will have played its part, but now with a difference. Instead of building up a mimetic likeness bit by bit it will merely have conserved and rendered numerically preponderant a likeness which had turned up quite independently. . . . Why variations on the part of one species should bear a strong resemblance to other, and often distantly related, species is another question. . . . The occurrence of mimetic resemblances is the expression of the fact that color pattern is dependent upon definite hereditary factors of which the total number is by no means very great. As many of the factors are common to various groups of butterflies, it is to be expected that certain of the color patterns exhibited by one group should be paralleled by certain of those found in another.

Upon examination these statements appear to embody a formal explanation of the facts to which it is difficult to take exception. Hence it must be admitted that this is perhaps the goal toward which with regard to this problem naturalists have been working for more than half a century. But while his hypothesis may be correct, its author's reasons for deeming it so seem quite insufficient.

The chief points of support on which it rests are the following, which are not arranged in the order of importance assigned to them:

1. The difficulty of finding the appropriate enemy which shall exercise the discrimination postulated by current hypotheses.

2. The alleged fact, mathematically demonstrated, that reciprocal mimicry between two species can not be established by selection of a long series of slight variations.

3. The theoretical difficulty of the initial variation in cases other than that above, for it seems reasonable that if the ancestral types from which mimic and model are derived were in the beginning very unlike in appearance

no slight departure from one in the direction of the other could have selective value.

4. The non-appearance of intermediates when a form which is assumed to have been derived from another by selection of a series of heritable variations (mutations) is crossed back with the original.

5. The apparent fact that the three females of the polymorphic oriental butterfly, *Papilio polytes,* occur in proportions which are approximately the same now as fifty, or possibly one hundred and fifty years ago, although it may be demonstrated mathematically that if either of the two mimetic forms possesses even a slight advantage over that from which they are assumed to be descended, this should have appeared in an altered ratio while they continue to live and breed together under the same conditions.

6. The fact that certain variations induced by differences in temperature or humidity are not directly inherited, since it is alleged that this limits the material upon which selection might be supposed to operate.

Of these points the first three may be more conveniently considered later with other common objections to current hypotheses of mimicry. The remaining three will be next examined in order.

Punnett accepts Fryer's[32] conclusion that in *P. polytes* the two supernumerary females which resemble *P. aristolochiæ* and *P. hector* differ genetically from the third female (which resembles the male) to the extent of one and two Mendelian factors, respectively. He cites the fact that there are forms of sweet peas, for example, which are known to have arisen as sudden sports, and behave in heredity as though they differed from the normal by a single factor. Hence he infers from analogy, first, that the two mimetic butterflies sprang from the primitive type by one or two mutations, as the case may be, and, as a corollary, that resemblance to their models was not attained by gradual shaping of their destinies through the accumulation of lesser variations by natural selection.

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[32] *Phil. Trans. Roy. Soc. Lond.,* Vol. 204 *B.*

But Castle[33] still contends vigorously that a single genetic character may undergo quantitative change under selection, and if this be true the difference finally attained by two forms differing only in one factor might follow from the accumulation of an indefinite number of slight variations. Still the complete abandonment of Castle's position would not save Punnett's argument. For if reported observations and inferences concerning *Drosophila*[34] are correct, a red-eyed strain has given rise to white by mutation and this in turn to eosin, which being crossed with the original red gave in the F_2 generation offspring in the proportion of three red to one eosin.

It is quite immaterial whether one explains these relations upon the hypothesis of multiple allelomorphs, or, as Punnett[35] prefers, upon the assumption of complete coupling of factors. In the former case one must admit that by breeding experiments the end product of a series of mutations can not be indubitably distinguished from one that results from a single modification of the affected factor. In the latter, one must grant that the occurrence of the grandparental types in the offspring of hybrid parents in the ratio of three to one is no proof that the grandparents themselves differed in respect to one character alone, or that the difference between the two resulted from changes occurring at one time in the germinal constitution of an ancestor of one of them. Hence, in so far as this argument is concerned, there is in the case of *P. polytes,* for example, no assured reason for supposing that the *aristolochia*-like form did not attain its present appearance by a series of steps, of which a number of the later at least were preserved by virtue of the advantage they conferred upon the individuals in which they appeared.

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[33] "Genetics and Eugenics," p. 188. Cambridge, Harvard University Press, 1916.

[34] Morgan, Sturtevant, Müller and Bridges, "The Mechanism of Mendelian Heredity," p. 164. New York, Henry Holt and Co., 1915.

[35] *Jour. of Genetics,* Vol. 5, pp. 37–50.

Little need be said regarding the inference that the constancy of the ratio in which the females of *P. polytes* seem to have occurred for many years shows that natural selection does not exist for this species in Ceylon, or else that its force is so slight that in half a century, and perhaps in a century and a half, it has produced no effect appreciable to the method of examination employed. This is valid only if it is true as postulated that the various types of *P. polytes* constitute "a population living and breeding together under the same conditions." But it is gravely to be doubted that this indispensable condition is fulfilled. We have some evidence (that of Bates and Wallace already cited) that butterflies which differ in color differ in habit, and if it should appear that the colors of butterflies in general are correlated with and repeat those of their surroundings, Punnett's fifth point is forever invalid. For it will be impossible to establish by observation the universal negative that is required, which is, of course, that the three types of female do not differ in any constant respect in their normal behavior.

Regarding the sixth point, which has reference chiefly to the fact of seasonal dimorphism among butterflies, it must first be affirmed that although the induced changes differentiating the broods of the spring and summer, or wet and dry seasons, are not directly inherited, the capability of responding definitely to the physical stimulus of changed temperature or humidity is a heritable racial trait.[36] The seasonal variations in the coloration of butterflies may be analogous upon the whole with the instantaneous color changes of tropical fishes, which also occur in response to external stimuli. The latter, however, follow more quickly than the former upon appropriate stimulation; they are reversible; and are known to be normally adaptive, since they reduce the conspicuousness of the individuals in which they appear. It may eventually prove to be a fact that instantaneous adaptive color adjustments, the phenomena of seasonal and sexual dimorphism, and polymorphism all have the same biological significance, *i. e.*, that they represent different ways in which the coloration of a species exercises its obliterative function in a greater variety of circumstances than would be possible if it were uniform. Upon this view of the matter there would seem to be no reason why color variations of the seasonal sort should not provide material for evolution by natural selection.

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[36] Professor Gerould first called attention to this fact in THE AMER. NAT., Vol. 50 (1916), pp. 310–316.

Before suggesting another possible explanation of the fact of mimetic resemblance it seems desirable to state more specifically why certain of those already mentioned seem improbable.

Some color patterns are apparently limited to fishes whose habits are similar. Others occur which have survived the introduction of marked structural changes and are now the common property of whole families or groups of families, whose manner of living varies decidedly from species to species. There is one such system of coloring among grunts, groupers and snappers (Hæmulidæ, Epinephelinæ, and Lutianidæ), and Labrids and Scarids share another. In each pattern modifications may be noted which seem particularly appropriate under the local conditions in which they appear. Individual elements may lose all semblance of the original, and yet the nature of the whole be not obscured. But these facts make one skeptical regarding Thayer's hypothesis, for if, in butterflies too, detail is less important than the appropriate effect of the whole, the probability is remote that for different environments complex, ideal, protective or concealing patterns exist, whose slightest spot is so significant that there is marked tendency for forms of different racial endowment to attain them, if their habits are similar.

The same facts militate against such a conception as Packard's, that mimicry is a result of similar reaction to the direct influence of one set of external conditions. For coloration is characterized by such conservatism or inertia, and the same elements of pattern appear in such a variety of habitats, that the power of environmental influence to induce uniformity of coloration seems discredited.

If the possibility of the direct influence of local climatic factors be excluded, Piepers' hypothesis, that mimicry is largely due to species having independently attained the same stage of development orthogenetically, leaves the facts of geographical distribution of mimics and their models enshrouded in mystery. That this is a very real difficulty follows from Punnett's statement,[37]

> Examples of close resemblance between butterflies which live in different parts of the world are relatively rare and serve to emphasize the fact that the great bulk of these resemblance cases are associated in pairs or little groups.

Finally, instances of mimicry are, after all, only selected examples of resemblance, and it is desirable, if possible, to formulate an explanation that will apply to all equally well. But whether the likeness between them rises by sporting or otherwise, it is not to be supposed that Phasmids and green leaves or dry twigs possess Mendelian factors in common. Therefore it seems profitable to proceed for a little upon the assumption that mimicry is in some cases at least a visible token of the fact that the species manifesting it are linked by some bond other than common descent, common habit, or exposure to the influence of a common environment. What this may be, does not appear, unless through mutual resemblance advantage accrues to some or all of the forms concerned.

Evidence compiled by Marshall[38] shows that birds undoubtedly attack butterflies, but others deny that they feed upon the insects freely enough to affect the evolution of their coloration, and more particularly the mimetic resemblances between different species. Hence there is plainly a question at issue concerning the sufficiency of an assigned cause to produce a stated effect. Under the circumstances any evidence tending to show that the frequency of birds' attacks has been underestimated, or that their influence may be supplemented by that of other enemies is of the greatest interest.

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[37] *L. c.*, p. 54.

[38] *Trans. Ent. Soc. Lond.*, 1909, pp. 329–383.

In this connection Swynnerton's[39] observation that of twenty small bird excreta collected in the African forest no less than eighteen contained scales and small wing fragments of Lepidoptera has suggestive value. But, for the moment at least, it is more important that it appears that mimicry might be initiated and advanced by indiscriminate feeders, including lizards and insectivorous insects, provided only that they possess color vision. For to whatever extent such influence prevails it obviates the necessity of appeal to the effects of discriminate feeding by birds or other animals, and makes it possible to forestall the criticism to which reference has been made above.

Therefore it is suggested as a tentative explanation of mimicry, that it has commonly arisen as a result of bionomic pressure applied first by discriminate or indiscriminate feeders, which by elimination of unadapted variants have forced their accustomed prey to assume color combinations which most effectually conceal it in its normal environment. In addition, for no demonstrated reason, in a few of the many thousands of cases in which colors adapted to the environment and habits of their possessor have been evolved, patterns have appeared which have been sufficiently like one another to deceive enemies which exercise discrimination in their choice of food. Beyond this point the evolution of resemblance may have proceeded according to accepted formulæ, but without conspicuousness being involved at any point in the process.

It is submitted that in our present state of ignorance this construction may be placed upon observed facts rationally and without exposure to the criticism that has been directed against other attempted interpretations. However, the chief classes of facts to be explained and the most serious objections registered against the Neo-Darwinian hypotheses of mimicry will be presented, that the reader may judge whether a passage between Scylla and Charybdis may be made in safety.

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[39] *Ibis,* 1912.

Professor Poulton's extensive studies have convinced him that the evolution of mimetic resemblance has been directed by natural selection,[40] yet the evidence upon which his conclusion rests may be taken over bodily and supports the revised hypothesis as consistently as that to whose service it was originally dedicated. There is nothing anomalous in finding mimic and model living under the same conditions, certain groups of insects showing the same series of local color varieties, or such diversity of coloration appearing in one group of butterflies or moths as allies them outwardly with different "protected" genera. The same is true of the fact that insects with every variety of larval experience as adults possess the same type of coloration, that mimetic females are more common than males, or that the common coloration possessed by mimic and model is attained in the most diverse fashion, that is, that cases of mimicry are typical instances of analogy. Throughout the whole series of observations the points of agreement and difference are consistent, as far as is known, with the fundamental assumption that color and habit are associated variables.

Passing to the negative side of the argument, we may first consider the statement that it is impossible that reciprocal mimicry should have been brought about by natural selection of small variations. Punnett has this idea from Marshall[41] and uses it to emphasize the difficulty of the initial variation even in cases where it might seem that the theoretical advantage to be gained from mutual resemblance by two species would simplify the attainment of likeness. But Dixey,[42] against whose position the argument was originally directed, has exposed its unsoundness by calling attention to a number of critical points which his opponent had failed to take into consideration.

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[40] See "Natural Selection the Cause of Mimetic Resemblance and Common Warning Colors" in "Essays on Evolution," 1908.

[41] *Trans. Ent. Soc. Lond.*, Vol. 45, pp. 93–142.

[42] *Trans. Ent. Soc. Lond.*, Vol. 45, pp. 559–583.

It may be added that Marshall's reasoning rests upon what is without much doubt a baseless assumption, for he follows Müller in postulating that two species of distasteful insects will lose the same absolute number of individuals through attacks of ignorant enemies which in the beginning recognize neither of them. As a matter of fact, if two species differing in no respect except appearance are represented in the same area by 100,000 and 5,000 individuals, respectively, as Marshall assumes, the chances are 20:1 that any animal making an independent test of the food resources of its environment would first meet the more abundant form. Unless it learns its lesson perfectly from a single experience, the chances are essentially the same that it will kill another butterfly of the same kind before it encounters one of the second distasteful sort. But if most inexperienced enemies learn at the expense of one species that *some butterflies are not edible,* it is scarcely to be supposed that they will undergo as many unpleasant experiences before they retain an impression of the disagreeable character of the other. Hence Marshall's criticism can not be considered at present a valid objection.

Packard[43] believed that the concept of Müllerian mimicry had been overextended. He thought that in accumulating so many examples of warning coloration in their "Bionomics of South African Insects" Marshall and Poulton[44] in particular attempted to prove too much. Why an association of some scores of species representing many orders of Mashonaland insects should be pivoted upon the bitter-flavored beetle, *Lycus,* though some members of the group seemed more amply protected from attack by birds and lizards, was not clear. Yet one dares not be dogmatic in such matters, for the wasp, *Pompilus,* though more adequately equipped for defense than any other member of the association, may have drifted toward it at a comparatively late date, when the relatively slight distastefulness of a large number of insects of one type of coloration subtended a larger angle in the consciousness of insectivorous animals than the greater unpalatability of any single form. However, the idea that what has been considered mimicry is too common, and that in general the most effectively protected types should be the nuclei of the Müllerian combinations, is certainly not wholly unreasonable.

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[43] *Proc. Amer. Philos. Soc.,* Vol. 43, p. 424.

[44] *Trans. Ent. Soc. Lond.,* Vol. 41.

One of the chief reasons for believing in the existence of warning colors, and particularly of common warning colors, is the fact that some families of insects have slight range of color and pattern compared with others. Mayer[45] found that "the 200 species of *Papilio* in South America display 36 distinct colors, while the 450 species of Danaoid Heliconidæ exhibit only 15," and that "there is no lack of individual variability among the species of the latter, yet as a whole they vary but little from the two great types of color-pattern represented by *Melinœa* and *Ithomia.*" To explain these facts he felt obliged to resort to Müller's hypothesis, but if instead of thinking of Ithomiinæ and Papilionidæ one considers Holocentridæ and Labridæ, an alternative solution appears. The squirrel fishes seem to be of red or reddish coloration the world over, but their habits are equally invariable, while the Labrids' diversity of coloring is no greater than that prevailing in the varied environments in which they live.

Such facts indicate the necessity of making detailed studies of the coloration of tropical Lepidoptera and correlating the facts discovered with the insects' distribution and behavior. When this is done there is reason to suppose that combinations of the same colors will be found upon animals of the same habit, which would have been as they are in many species, if any or all the others which display the same combinations had never existed. That is to say, it is probable that much that has masqueraded as Müllerian mimicry is nothing but the result of convergent evolution, which has been difficult to explain because of the deep-seated misconception that has prevailed regarding the function of animal coloration.

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[45] *Bull. Mus. Comp. Zool. Harv. Coll,* Feb., 1897, p. 225.

Dewar and Finn[46] cite a number of instances of resemblance between mammals, and others between birds, whose ranges coincide at no point. For the most part these likenesses do not seem comparable with the clearest cases of mimicry among insects in the degree of detailed resemblance they involve, and scarcely seem to rise above the level of interesting coincidences. It is unquestionably true, nevertheless, that such degree of likeness as may spring up between two species whose bionomic association is impossible on account of differences in geographical distribution, may also arise between species of one region without reference to the action of natural selection directed toward the production of resemblance.

Lock[47] states that Syrphid flies, which closely mimic small bees and wasps whose habits are similar to their own, are surprisingly numerous in southern Japan, and that their resemblance to bees is particularly noticeable, though these are conspicuous by their absence. Hence the question arises, how the flies can benefit by their resemblance to them: to which one must apparently answer, that under the conditions stated, the bee-like disguise can, as such, be of little value. But this query is overshadowed in interest by another: If the Syrphids are unprotected and driven by their enemies to assume the appearance of defended forms, how do they survive in regions where their disguise possesses no suggestion of unpalatability.

The idea is not to be entertained for a moment that Lock would be at a loss for an answer. But if the concept of warning coloration be abandoned, there is no reason to suppose bees less perfectly adapted in color and form than other animals to their respective modes of life. Bee-like flies whose habits resemble those of bees should therefore be well able to exist beyond the range of models, which they may have mimicked in other times and places, if their particular type of coloration is as well suited to the new environment as to the old.

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[46] "The Making of Species," pp. 242–245. London and New York, J. Lane, 1909.

[47] "Recent Progress in the Study of Variation, Heredity and Evolution," p. 58. London, John Murray, 1907.

An apparent inconsistency in the Batesian and Müllerian hypotheses as at present interpreted has been frequently noted by hostile critics. To Reighard[48] it appears, for example, that if insectivorous vertebrates have pushed the resemblance between mimics and their models to the point of apparent identity, ordinary specific differences should suffice to warn them of the unpalatability of prospective and familiar prey.

This objection is so fairly met by the revised hypothesis, and the ground for criticism so completely removed, that further comment is unnecessary. But even when no inconsistency is involved in the explanation of the facts, some will doubtless consider the resemblance of the mimic to its model, or of insects to other objects, hypertelic. It is doubtful, however, whether hypertely embodies a real difficulty. For just as two streams flowing down a tolerably smooth inclined plane of infinite length will eventually unite, if all deviations of one or both which exceed a given magnitude are blocked when they tend to increase the distance between them, so, if heritable variations in the color and pattern of a given mimic are distributed according to Quetelet's law, for example, and only the extreme forms most unlike the model be eliminated in successive generations, closer and closer resemblance between the two may appear and approach identity without appeal to that over-refinement of vision whose existence among insects' enemies is at least problematical.

It is a standing objection to the mimicry hypotheses, and indeed to the explanation of any highly complex adaptation by natural selection, that at every stage the degree of resemblance attained must have been serviceable in order to assure its survival. It is understood, however, that this objection is applicable only to stages

[48] Carn. Inst. Wash., *Papers from Tortugas Lab.*, Vol. 2, p. 315.

following the first to which the selectionist ascribes deceptive value. Resemblance resulting from undirected variation, or existing for other reasons, is not subject to this criticism.

Darwin recognized this fact and attempted to throw upon another cause than natural selection a large part of the burden of producing functional resemblance. His idea may best be expressed in his own words:

> The process of imitation probably never commenced between forms widely dissimilar in color. But, starting with species already somewhat like each other, the closest resemblance, if beneficial, could readily be gained by the above means (natural selection), and if the imitated form was subsequently and gradually modified through any agency, the imitating form would be led along the same track, and thus be altered to almost any extent, so that it might ultimately assume an appearance or coloring wholly unlike that of the other members of the family to which it belonged. There is, however, some difficulty on this head, for it is necessary to suppose in some cases that ancient members belonging to several distinct groups, before they had diverged to the present extent, accidentally resembled a member of another and protected group in sufficient degree to afford some slight protection, this having given the basis for the subsequent acquisition of the most perfect resemblance.[49]

Weismann[50] attempted to avoid the same difficulty in another way. He makes no assumption that the original difference betwen mimic and model was distinctly less than that appearing at present between typical members of their respective families, but magnifies the importance of the first slight resemblance and subsequent positive variations. He had been deceived repeatedly, at least for the moment, by similarity in the flight of different species whose colors were not the same, and held as a consequence that mere variation in the manner of flight combined with the habit of associating with the form mimicked might have prepared the way for selection.

Wallace[51] would have it that certain butterflies, having become unpalatable through the possession of disagreeable juices, developed distinguishing marks, whether in color, form or mode of flight. He then plunges *in medias res* with the assertion that "during the early stages of this process, some of the Pieridæ, inhabiting the same district, happened to be sufficiently like some of the Heliconidæ to be occasionally mistaken for them." Thereafter, as may be anticipated, evolution proceeded merrily, and examples of Batesian mimicry were perfected in due time.

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[49] ''Origin of Species,'' Chap. XIV.

[50] ''The Evolution Theory,'' Vol. 1, p. 93. London, Edward Arnold, 1904.

[51] ''Darwinism,'' p. 243.

Wallace's pronouncement begs the whole question. Weismann's hypothesis is conceivably true, but lacks the support necessary to carry conviction. Darwin's idea, finally, seems to be at variance with fact, since Poulton[52] infers from his own studies that the conclusion that emerges most clearly is the entire independence of zoological affinity exhibited by mimetic resemblance.

Punnett also shows most clearly how impossible the Darwinian suggestion is, but errs when he supposes that it can not be true in many cases that model and mimic were closely alike to start with. His demonstration may be accepted that the development of mimetic resemblance has not been commonly facilitated by preexisting likeness due to racial affinity, but he has wholly disregarded the fact that the degree of likeness which it is necessary to presuppose, if mimicry has been brought about by a series of comparatively small variations, might occur for other reasons.

May we not assume,[53] for example, that the Pieridæ and Heliconidæ are usually distinctly different in their habits, and that the coloration of typical members of each group is a combination of hues well suited upon the average to render them inconspicuous in such places as they commonly frequent. If this be so, the initial step toward the production of new cases of mimicry might be any one of many variations in mode of nutrition or reproduction, which would lead representatives of the first family to spend their lives after the manner of the second. Reason has already been given for believing that convergence in color would probably accompany or follow convergence in habit.

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[52] *Proc. Linn. Soc. Lond.*, Vol. 26, p. 570.

[53] This can scarcely be considered a rash assumption, since Wallace states (*Trans. Ent. Soc. Lond.*, Vol. 2, Ser. 2) that the Pieridæ of the Amazon valley generally are open-ground butterflies, two genera only, *Leptalis* and *Terias*, being true denizens of the forest. He also remarks that most of the species of *Heliconia* prefer the forest shades. It is also of interest to note that he comments upon the *inconspicuousness* of some species at least of *Ithomia*, in which connection one should recall the observation of W. J. Kaye already quoted.

The new colors would undoubtedly appear in patterns largely determined by and reflecting the Pierian ancestry. Among fishes, as has been stated, a primitive color pattern peculiar to one or common to several closely related families is sometimes readily recognizable, in which distinct elements are apparent, now definite, now diffuse, mere stains of dyes that are not permanent. It is to be expected no less in insects that the family patterns, like finely wrought ornaments cast into the melting-pot, will be reshapen and serve new purposes. But from the welter of change and recombination which this involves may come once in many times a new grouping of characters, which suggests the pattern of another race. At this point natural selection directed toward the production of a protective design painted in colors appropriate to the environment may yield to selection working in the direction of resemblance. If so, a new pattern may be developed in the same protective colors and coupled with such change in the shape of the wings, or in other characters, as confers the additional advantage of being mistaken for a species which enjoys some measure of immunity.

Either in organization or development most animals give evidence of changes in habit much greater than the initial one herein postulated. Yet admit that these may occur, and what is already partly proved, that color is correlated with habit throughout the animal kingdom, and a theoretical difficulty that has engaged the attention of adherents and opponents of the mimicry hypotheses vanishes. No matter how wide the original gap between mimic and model, it may be bridged; no matter what degree of similarity between two forms may be necessary before natural selection may become effective in heightening their resemblance, it may be attained without appeal to chance that is wholly blind, for there appears to be an automatic feature in the mechanism which has hitherto escaped observation.

The ideas outlined in the preceding pages are neither a pure product of reflection nor a compromise suggested by an examination of the literature upon mimicry. They are a normal outgrowth of studies which had no preconceived relation to the problem of mimetic resemblance. They constitute a working hypothesis, and as such are submitted to those biologists, particularly entomologists, who may have opportunity to test them rigorously.